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# WORK AND POWER OUTPUT IN THE HINDLIMB MUSCLES OF CUBAN TREE FROGS *OSTEOPILUS SEPTENTRIONALIS* DURING JUMPING

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## Summary

**It has been suggested that small frogs use a catapult mechanism to amplify muscle power production during the takeoff phase of jumping. This conclusion was based on an apparent discrepancy between the power available from the hindlimb muscles and that required during takeoff. The present study provides integrated data on muscle contractile properties, morphology and jumping performance that support this conclusion. We show here that the predicted power output during takeoff in Cuban tree frogs *Osteopilus septentrionalis* exceeds that available from the muscles by at least sevenfold. We consider the sartorius muscle as representative of the bulk of the hindlimb muscles of these animals, because this muscle has properties typical of other hindlimb muscles of small frogs. At 25 °C, this muscle has a maximum shortening velocity ($V_{max}$) of 8.77±0.62 $L_0$ s$^{-1}$ (where $L_0$ is the muscle length yielding maximum isometric force), a maximum isometric force ($P_0$) of 24.1±2.3 N cm$^{-2}$ and a maximum isotonic power output of 230±9.2 W kg$^{-1}$ of muscle (mean ± S.E.M.). In contrast, the power required to accelerate the animal in the longest jumps measured (approximately 1.4 m) is more than 800 W kg$^{-1}$ of total hindlimb muscle. The peak instantaneous power is expected to be twice this value. These estimates are probably conservative because the muscles that probably power jumping make up only 85 % of the total hindlimb muscle mass. The total mechanical work required of the muscles is high (up to 60 J kg$^{-1}$), but is within the work capacities predicted for vertebrate skeletal muscle. Clearly, a substantial portion of this work must be performed and stored prior to takeoff to account for the high power output during jumping. Interestingly, muscle work output during jumping is temperature-dependent, with greater work being produced at higher temperatures. The thermal dependence of work does not follow from simple muscle properties and instead must reflect the interaction between these properties and the other components of the skeletomuscular system during the propulsive phase of the jump.**

Key words: jumping, power output, contractile properties, skeletal muscle, Cuban tree frog, *Osteopilus septentrionalis*, force–velocity curve, temperature, $Q_{10}$.

## Introduction

The limits to the production of mechanical work and power have long been a fundamental focus of research on skeletal muscle. Recent studies have shifted attention from purely *in vitro* studies of muscle performance to an integrated approach that links *in vitro* and *in vivo* performance (Marsh *et al.* 1992; Altringham *et al.* 1993; Rome *et al.* 1993; Marsh and Olson, 1994). Animals that have evolved as effective jumpers provide an excellent system for extending this approach. Jumping as a specialized form of locomotion is employed by a variety of vertebrates and invertebrates (Bennet-Clark, 1977; Emerson, 1985). Maximizing jumping distance (or height) requires that a large amount of mechanical power be delivered during takeoff (Bennet-Clark, 1977; Marsh, 1994). The requirement for high power output may not at first be obvious from simple ballistics formulae that predict that jumping distance is directly proportional to the mechanical work done during takeoff. However, the distance through which the center of mass moves during takeoff is fixed by the linear dimensions of the frog. Thus, the more force that is applied to increase the kinetic energy of the animal, the sooner the animal leaves the ground. Because mechanical power is work per unit time, these rapid takeoffs require high power output. The simple physics of the jump makes it possible to calculate accurately the work and average power during takeoff from simple measurements of jumping distance combined with morphological measurements (Marsh, 1994). These measurements can then be compared with estimates derived from *in vitro* contractile studies.

We used frogs to investigate *in vitro* and *in vivo* performance during jumping. Jumping is the primary form of locomotion of many frogs. Frog hindlimb muscles are easy to work with *in vitro*, and studies of these muscles have contributed greatly to our understanding of contractile mechanisms in skeletal muscle (Woledge *et al.* 1985). Additionally, many studies have reported jumping distances in various species (references in

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Marsh, 1994), and a few studies have attempted to look at the detailed mechanics of jumping (Calow and Alexander, 1973; Hirano and Rome, 1984; Marsh and John-Alder, 1994). Species that are arboreal or terrestrial are among the best jumpers (Zug, 1978), and we chose to work with the Cuban tree frog *Osteopilus septentrionalis*.

Marsh and John-Alder (1994) calculated power output of the hindlimb muscles of hylid frogs on the basis of measurements of takeoff velocity and jumping distance at 20 °C. They obtained values for the average power produced during takeoff that ranged from 30 to 90 W kg$^{-1}$ of body mass. The energy to produce the jump in frogs must come from the hindlimb muscles. The jump is a standing jump with no countermovement. The muscles in the back that act to extend the sacral joint are active during jumping (Emerson and De Jong, 1980), but in total these muscles are very small, amounting to less than 0.5 % of body mass. The forelimbs are also quite small and are almost fully extended before the jump begins. Hindlimb muscles in hylids were estimated to occupy between 14 % and 18 % (Taigen *et al.* 1985; Marsh and Taigen, 1987) of the total body mass ($M_b$). Therefore, if power were to come directly from these muscles during takeoff, they would have to produce an average power of at least 500 W kg$^{-1}$ to achieve the highest levels of performance measured.

However, power production is not uniform during the takeoff phase of the jump. The power required to accelerate the frog rises to a peak late in the takeoff phase, then falls off rapidly just prior to takeoff (Calow and Alexander, 1973; Marsh and John-Alder, 1994). As a result, peak power is actually approximately twice the average power (Marsh, 1994; M. M. Peplowski and R. L. Marsh, unpublished data). Thus, Marsh and John-Alder (1994) estimated that if the muscles were directly powering the jump, they would have to produce a peak power in excess of 1000 W kg$^{-1}$. Furthermore, this calculation assumes that all of the hindlimb muscles are used equally to power the jump. In fact, a number of muscles antagonize those used for jumping (Dunlap, 1960; Matsui, 1978) and probably provide little or no power for the jump. Therefore, this estimate of power output is probably conservative.

These impressively high estimates of power output do not coincide with those obtained in several *in vitro* isotonic contractile studies on isolated frog skeletal muscle (Marsh, 1994). The highest peak power values recorded *in vitro* at 20–25 °C are approximately 370 W kg$^{-1}$ (Lännergren *et al.* 1982; Lutz and Rome, 1994) and most estimates are considerably lower (Marsh, 1994). On the basis of these earlier studies, an apparent discrepancy of more than 600 W kg$^{-1}$ exists between the *in vivo* and *in vitro* estimates of power output.

The conclusions of Marsh and John-Alder (1994) remain somewhat tentative because the data for jumping distance, muscle mass and contractile properties were obtained from different animals. The possibility exists that the maximal jumps recorded were produced by unusually 'athletic' frogs having either larger than average muscle masses or muscles with unusual contractile properties. In the present study, we measured jumping performance, animal dimensions and contractile properties using the same group of Cuban tree frogs (*Osteopilus septentrionalis*). These measurements allowed us to define more precisely the relationship between *in vitro* and *in vivo* muscle performance. We hypothesized that power outputs during takeoff, estimated from jumping distance and the morphology of the frogs, would greatly exceed those obtained in isotonic contractile studies.

We used temperature as a variable to influence performance. Jumping performance improves with increasing body temperature ($T_b$) up to the frog's thermal limit (John-Alder *et al.* 1988). Temperature also influences muscle power output (Renaud and Stevens, 1984). However, Marsh (1994) reviewed data suggesting that temperature effects *in vivo* are smaller than those found *in vitro*. Given this background information, temperature becomes an important variable in part because the magnitude of the difference between *in vivo* and *in vitro* power output may depend on the temperature chosen for the measurements.

## Materials and methods

### *Animals*

Cuban tree frogs *Osteopilus septentrionalis* (Duméril and Bibron), collected in Florida, USA, were obtained from a commercial supplier. Two groups (16 animals in total) were used, one group obtained in August and the other in October. The frogs were studied within 4 weeks of their arrival in the laboratory. The animals were kept in aquaria with moistened sphagnum moss and a water source. The frogs were maintained on a 12 h:12 h L:D cycle at temperatures ranging from 25 to 28 °C. They were fed crickets supplemented with powdered vitamins and calcium carbonate two or three times per week. Immediately after obtaining the animals from the supplier, measurements were made of each animal's body mass ($M_b$) in grams, snout–vent length ($L_{sv}$) and hindlimb length ($L_{hl}$) in millimeters, as well as the distance from the sacral joint to the vent ($L_{sac}$), in millimeters. The mean values ± S.E.M. for these measurements were 12.9±1.4 g, 63.2±2.4 mm, 85.9±3.0 mm and 27.5±1.0 mm for $M_b$, $L_{sv}$, $L_{hl}$ and $L_{sac}$, respectively. The range of body masses used (7–16 g), was large enough to produce a small allometric effect on jumping distance. This effect was revealed by analysis of the residuals around the regression given in Fig. 1 (data not shown) and was consistent with previous analyses (Marsh, 1994). The range of body masses of the animals used would be expected to cause an approximately 15 % change in jumping performance from the smallest to the largest frogs. However, because our calculations of power output rely on individual values for each frog, allometric effects were not considered further in the present study.

### *Jumping*

Frogs jumped in a temperature-controlled 2.3 m×3.6 m room. The frogs were placed individually in containers with

50–100 ml of water. Each container was then placed in a water bath on the floor of the temperature-controlled room and allowed to equilibrate at the experimental temperature for approximately 2 h before the jumping trials began. The floor of the room was covered with brown packaging paper. The tree frogs seemed to have excellent traction on this surface. The belly of each frog was painted lightly with food coloring immediately before its jumping trial began. In most cases, a series of 10 jumps was recorded in a trial. In a few instances, the frog exited the testing area before completing 10 jumps. The minimum number of jumps recorded in a trial was six. The distance between successive dye marks on the packaging paper was measured and recorded as jumping distance. Immediately after a jumping trial, the animal's cloacal temperature ($T_b$) was measured using a vinyl-coated thermocouple probe. The mass of the frog was then measured to the nearest 0.1 g using a Mettler balance. One set of jumping trials took place in the morning, followed by a rest period of at least 3 h, and then another set of jumping trials at the same air temperature in the afternoon. On different days, air temperature in the room was set at approximately 15, 20, 25 or 30 °C. However, body temperatures during each set of jumping trials varied among the frogs, perhaps due to the frogs' position in their containers before jumping and to variations in the temperature and humidity of the room. Frogs can cool below air temperature due to evaporation from their moist skin. We thus obtained a fairly continuous range of $T_b$ from 11.5 to 31 °C among the various trials. All 16 frogs were jumped at each air temperature.

### *Contractile studies*

The procedure followed was similar to that of Olson and Marsh (1992). The final body mass of the frog was obtained and the animal killed by pithing. The sartorius muscle from one hindlimb was removed, attached to an ergometer lever (Cambridge Technology, model 305), and immersed in recirculating amphibian Ringer's solution (115 mmol $l^{-1}$ NaCl, 2.5 mmol $l^{-1}$ KCl, 1.0 mmol $l^{-1}$ $MgSO_4$, 20 mmol $l^{-1}$ imidazole, 1.8 mmol $l^{-1}$ $CaCl_2$, 11 mmol $l^{-1}$ glucose, pH 7.9) saturated with 100 % $O_2$. Supramaximal stimuli of 0.2 ms duration were produced by a power amplifier slaved to a Grass S48 stimulator. Stimuli were delivered to the muscle *via* two platinum plate electrodes on opposite sides of the muscle. The muscle was set at the length ($L_0$) which yielded the maximum force ($P_0$ in N $cm^{-2}$) during an isometric tetanus. After measuring isometric properties at a given temperature, the muscle was then subjected to a series of isotonic contractions, decreasing stepwise in force from $P_0$ to approximately 3 % of $P_0$. Isometric force was measured in the middle and at the end of this isotonic series. If force had declined by less than 15 % of the initial $P_0$ measured at that temperature, the muscle temperature was changed, and the isometric and isotonic contractions were repeated. Contractile studies were performed on muscles from nine of the 16 frogs used in the jumping measurements. Each of these muscles was measured initially at 20 °C for isometric properties and then at 1–3 other temperatures for isotonic properties. All muscles were measured at either 20 or 25 °C for isotonic properties.

Each muscle studied *in vitro* was measured at several temperatures in a series. Thus, in estimating $P_0$, the effects of fatigue need to be distinguished from the effects of temperature. Acute temperature effects were estimated by measuring $P_0$ immediately before and after each temperature change. The value just before the temperature change was used to estimate the level of fatigue at that point in the series. The $P_0$ values measured later in the series of measurements were adjusted upwards to their approximate prefatigue levels.

Isotonic force–velocity curves were generated by fitting the data with the hyperbolic–linear equation of Marsh and Bennett (1986*a*):

$$V = \frac{B(1 - P/P_0)}{A + P/P_0} + C(1 - P/P_0)\,, \qquad (1)$$

where $V$ is shortening velocity in $L_0\,s^{-1}$, $P$ is force in N $cm^{-2}$, $B$ and $C$ are constants with dimensions of $L_0\,s^{-1}$ and $A$ is a dimensionless constant. Statistical fitting was carried out using the non-linear curve-fitting routines in the application Igor for the Macintosh computer. The shape of the force–velocity curve was described using the dimensionless power ratio ($R_P$), which is equal to the maximum isotonic power divided by the product of $V_{max}$ and $P_0$ (Marsh and Bennett, 1986*a*).

### *Muscle masses*

Following the jumping trials and muscle contractile studies, several muscles from one moist hindlimb of each animal were dissected out separately and the wet mass measured (to nearest milligram) using an enclosed Mettler balance. Any remaining muscle was scraped free from the bone and weighed. Muscle masses of each animal were obtained within 24 h of killing the animal.

### *Calculations*

The calculations of jumping performance used in the present study are based on formulae given in Marsh (1994). The simple ballistics of frog jumping permit calculation of the *in vivo* work and power output based on total jumping distance ($L_j$). Using ballistics formulae, the following equation for jumping distance is derived:

$$L_{j,l} = \frac{V_t^2 \sin 2\theta}{\boldsymbol{g}}\,, \qquad (2)$$

where $L_{j,l}$ is the level distance traveled by the center of mass between the time of takeoff and the time it returns to the takeoff height, $V_t$ is the takeoff velocity in m $s^{-1}$, $\boldsymbol{g}$ is the acceleration due to gravity (9.81 m $s^{-2}$), and $\theta$ is the angle of takeoff, assumed here to be 40 ° for maximal jumps. Considering the range of jumping distances obtained in this study for *Osteopilus septentrionalis*, the optimum angle for maximum jumping distance was calculated to be approximately 40 ° (Marsh, 1994). Precise determination of takeoff angle is not required because frogs can take off over a broad range of

angles and still achieve nearly maximal performance (Marsh, 1994). In the context of the present study, assuming an optimum takeoff angle is conservative because other angles would increase the power required to achieve a given jumping distance. $L_{j,l}$ can be approximated as:

$$L_{j,l} = L_j - 1.414L_{cm}, \quad (3)$$

where $L_{cm}$ is the distance from the tip of the toes to the center of mass along the outstretched hindlimb (see also equation 4). This calculation accounts for the horizontal distance moved before takeoff and at the end of the jump after the frog has descended below the takeoff height.

Equation 2 and the dimensions of the frog can then be used to calculate the body-mass-specific energy ($J\,kg^{-1}$) expended during takeoff. Equation 2 is rearranged to calculate $V_t$ and the kinetic energy ($E_k$) as $0.5V_t^2$. The potential energy ($E_p$) is calculated as $L_{cm}\boldsymbol{g}\sin\theta$ and the total work done ($W_j$) as $E_k$ plus $E_p$.

To determine the power output during the jump, the contact time ($t_c$), the time the frog spends on the ground from the beginning of the movement of the center of mass until takeoff, is first calculated as:

$$t_c = \frac{2L_{cm}}{V_t}. \quad (4)$$

The length used in this calculation represents the approximate distance traveled by the center of mass during the takeoff period. This length is longer than the hindlimbs because of the extremely flexed position of the hindlimbs before the jump. The center of mass initially is approximately over the feet when the frog is sitting before the jump (Hirsch, 1931). For our calculation, we have estimated $L_{cm}$ as $L_{hl}+0.67L_{sac}$. The position of the center of mass changes slightly during takeoff, moving posteriorly and ventrally as the hindlimbs are extended. We have ignored this movement because its effect is to decrease the calculated $t_c$ and thus increase the calculated power. Because of the nature of the comparisons made in the present study between *in vivo* and *in vitro* power output, we prefer to be conservative in our assumptions regarding power output during the jump. After estimating $t_c$, the power generated by the animal during takeoff is then calculated simply as:

$$\dot{W}_{j,b} = W_j/t_c, \quad (5)$$

where $\dot{W}_{j,b}$ is the power in $W\,kg^{-1}$ of body mass. This calculated power is the average value during the takeoff period. The peak power is expected to be approximately twice this value. The muscle-mass-specific power output is:

$$\dot{W}_{j,m} = \dot{W}_{j,b}/M_{hlm}, \quad (6)$$

where $\dot{W}_{j,m}$ is the power in $W\,kg^{-1}$ of hindlimb muscle mass and $M_{hlm}$ is the mass of the hindlimb muscles of the frog expressed as a fraction of the total body mass.

Equation 6 assumes that all of the hindlimb muscles are used to power the jump. However, this assumption is probably incorrect (Matsui, 1978; Marsh, 1994). Therefore, values calculated using equation 6 are expected to be minimum estimates of power output.

## Results

### *Jumping distance*

Most jumps undertaken by frogs in a laboratory setting are submaximal (Marsh, 1994). Thus, jumping studies often report the maximal jumps obtained in a series. Because we were interested in maximal performance, we report here the longest jump for each animal on each testing day (usually the longest of 20 jumps, see Materials and methods). Considerable variation existed in the maximal jumping performance of individual frogs on different days, and no significant rank-order correlation was found between individual and jumping distance. Maximal jumping distance ($L_j$) increased with increasing $T_b$. In Fig. 1, $\log L_j$ *versus* $T_b$ is fitted to a second-order polynomial ($P<0.0001$). This line describes what other authors have referred to as the mean maximal jumping distance. As indicated by the curvilinear relationship on semilogarithmic coordinates, the thermal dependence of $L_j$, expressed as an $R_{10}$ (Bennett, 1984), decreased with increasing temperature, from 1.51 in the interval 15–20 °C, to 1.3 between 25 and 30 °C. Similar results were obtained for this species by John-Alder *et al.* (1988). The body-mass-specific work performed during each jump is directly proportional to jumping distance, and is indicated on a second vertical axis in Fig. 1.

### *Muscle masses*

The total hindlimb muscle mass ($M_{hlm}$) was 16.7±0.52 % of body mass (mean ± S.E.M.) in *Osteopilus septentrionalis*. $M_{hlm}$ was significantly correlated ($P<0.04$) with the residuals from the regression shown in Fig. 1, indicating that a portion of the variability in jumping distance can be explained by variation in the mass of the hindlimb muscles as a percentage of body mass. However, presumably because of the variability in the jumping performance of individual frogs on different days, the

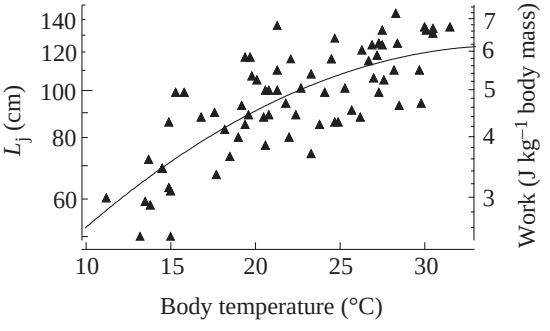


Fig. 1. Jumping distance and work as a function of body temperature for the Cuban tree frog *Osteopilus septentrionalis*. Maximum distance jumped ($L_j$) by an animal on a given day is plotted on a semilogarithmic scale as a function of body temperature. The data are fitted to a second-order polynomial: $\log L_j = 1.356 + 0.0421T_b - 0.0006T_b^2$ ($P<0.0001$, $r^2=0.61$). This line describes what other authors have called the mean maximal jumping distance.

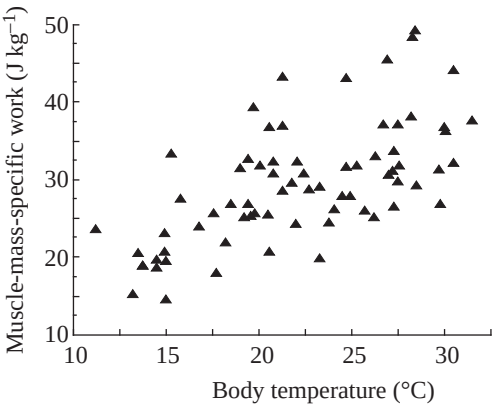


Fig. 2. Muscle-mass-specific work output of *Osteopilus septentrionalis* as a function of body temperature. Values were converted to muscle-mass-specific work ($W_{j,m}$) using body-mass-specific ($W_{j,b}$) values (Fig. 1) and hindlimb muscle masses ($M_{hlm}$) of the frogs.

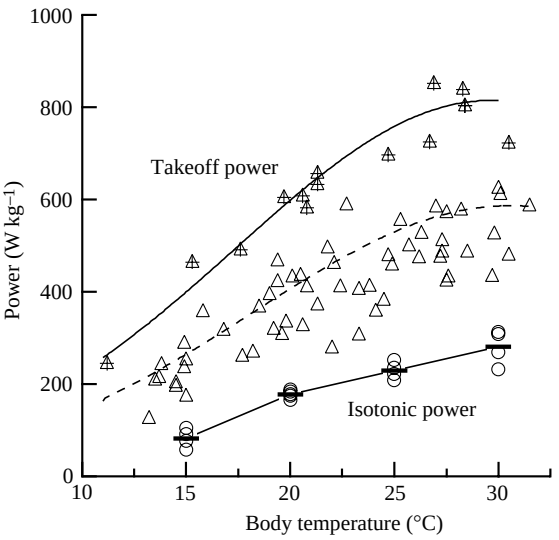


Fig. 3. Muscle-mass-specific power output in *Osteopilus septentrionalis*. Triangles represent the takeoff power predicted from the jumps shown in Fig. 1 using individual values of hindlimb length, body mass and muscle mass for each animal. The dashed line represents a polynomial regression through all of the data using log-transformed values for power output (see Results for further details). The solid line represents a similar regression through the highest 20 % of the data (triangles marked with crosses). The open circles are maximal isotonic power measured *in vitro* with the mean values marked with horizontal bars.

variation in $M_{hlm}$ only explained 6 % of the variation in jumping performance at different $T_b$. The summed masses of the muscles that are most likely to power jumping (Marsh, 1994) (the plantaris longus, peroneus, cruralis, gluteus magnus, semimembranosus, gracilis and adductor magnus muscles) made up an average of 85 % of the mass of the hindlimb muscles.

### *Work and power output during jumping*

Fig. 1 shows values for *in vivo* work output which are body-mass-specific. After conversion to muscle-mass-specific work, these values range from 14.4 to 49.8 J kg$^{-1}$ (Fig. 2). If only 85 % of the hindlimb muscle mass provides the energy for the jump, then the highest work outputs are approximately 60 J kg$^{-1}$.

Using the equations given above, we calculated muscle-mass-specific power outputs based on individual values for maximal jumping distance, hindlimb length, body mass and muscle mass for each frog (Fig. 3). To make comparisons of the *in vivo* and *in vitro* data, Fig. 3 is plotted using linear axes. However, statistical curve-fitting was carried out on the log-transformed values of jumping power *versus* $T_b$ because the log-transformed data satisfy the assumption of homoscedasticity.

As with jumping distance, power output increased with increasing body temperature. We used these data to define two performance levels. First, the mean takeoff power ($\dot{W}_t$) output was defined as the power predicted by the regression line through all of the data ($\log\dot{W}_t = 1.4270 + 0.0869T_b - 0.00142T_b^2$, $r^2 = 0.619$, $P < 0.0001$). Second, the maximal takeoff power ($\dot{W}_{t,max}$) output was defined by a regression line through the highest 20 % of the data across all temperatures ($\log\dot{W}_{t,max} = 1.645 + 0.0854T_b - 0.00144T_b^2$, $r^2 = 0.964$, $P < 0.0001$). (The data points used in this second regression analysis were those with the highest 20 % of the residuals from the first regression analysis.) Maximal power output increases with temperature, reaching values of approximately 800 W kg$^{-1}$ at 30 °C. Note that these values represent the predicted power averaged throughout takeoff, not the peak instantaneous power outputs, which are expected to be approximately twice these values.

### *Contractile properties*

Temperature had relatively small effects on $P_0$, which was essentially identical at 20 and 25 °C (Table 1). The mean $P_0$ for muscles at these temperatures was approximately 24 N cm$^{-2}$ (Table 1). The $P_0$ was an average of 15 % and 9 % lower at 15 and 30 °C, respectively. Using a paired comparison

Table 1. *In vitro isometric contractile data for the sartorius muscle of* Osteopilus septentrionalis

| $T_m$ (°C) | $N$ | $P_0$ (N cm$^{-2}$) | $t_{P,tw}$ (ms) | $t_{50\%R}$ (ms) | $P_{tw}/P_0$ |
|---|---|---|---|---|---|
| 15 | 4 | 19.6±1.2 | 46.1±2.20 | 60.1±3.51 | 0.665±0.024 |
| 20 | 9 | 24.4±1.9 | 29.0±0.94 | 38.3±3.02 | 0.710±0.025 |
| 25 | 4 | 24.1±2.3 | 20.3±0.48 | 27.0±3.87 | 0.610±0.075 |
| 30 | 5 | 21.9±1.4 | 16.2±1.04 | 18.8±2.09 | 0.562±0.045 |

$T_m$, muscle temperature; $N$, sample size; $P_0$, maximum isometric force; $t_{P,tw}$, time to peak force in a twitch; $t_{50\%R}$, time from peak force to 50 % relaxation in a twitch; $P_{tw}/P_0$, ratio of twitch force to tetanic force.

Values are means ± S.E.M.

Table 2. *Temperature effects on* in vitro *and* in vivo *muscle performance in the Cuban tree frog* Osteopilus septentrionalis

| | $Q_{10}$ | | |
|---|---|---|---|
| | Temperature interval (°C) | | |
| | 15–20 | 20–25 | 25–30 |
| *In vitro* contractile properties | | | |
| $V_{max}$ | 2.82 | 1.68 | 1.55 |
| $\dot{W}_{iso}$ | 4.77 | 1.65 | 1.50 |
| $1/t_{P,tw}$ | 2.52 | 2.04 | 1.57 |
| $1/t_{50\%R}$ | 2.46 | 2.01 | 2.06 |
| *In vivo* power output | | | |
| $\dot{W}_{j,m}$ | 2.35 | 1.70 | 1.22 |

The effects of temperature, represented by $Q_{10}$ values, are shown over three temperature intervals for mean *in vitro* contractile properties and *in vivo* power output during takeoff based on the power predicted by the regression line through all of the data in Fig. 3.

$V_{max}$, maximum isotonic velocity; $\dot{W}_{iso}$ maximum isotonic power; $t_{P,tw}$, time to peak force in a twitch; $t_{50\%R}$, time from peak force to 50 % relaxation in a twitch; $\dot{W}_{j,m}$, muscle-mass-specific power output during take-off.

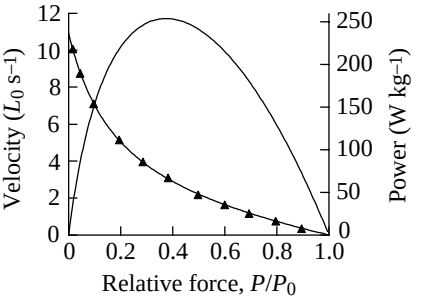


Fig. 4. Representative force–velocity curve for the sartorius muscle of *Osteopilus septentrionalis* at 30 °C. The data are fitted to the hyperbolic–linear equation of Marsh and Bennett (1986a) (see Results for further details). Isotonic power output (in W kg$^{-1}$ muscle) is shown as a function of force on the right-hand axis.

of values before and after temperature transitions, the $P_0$ at 15 °C was significantly lower than the value at 20 and 25 °C (paired $t$=4.425, $P$<0.02), but the $P_0$ at 30 °C was not significantly different from the value at 20 and 25 °C (paired $t$=1.81, $P$=0.17).

Mean isometric twitch times, the time to peak force ($t_{P,tw}$) and the time from the peak force to 50 % relaxation ($t_{50\%R}$), both in milliseconds (Table 1), decreased with increasing temperature ($r^2$=0.92 for log$t_{P,tw}$ *versus* temperature and $r^2$=0.80 for log$t_{50\%R}$ *versus* temperature). The $Q_{10}$ values for the reciprocal of these time parameters were high (1.6–2.5) over the entire temperature range studied (Table 2).

A representative force–velocity curve is shown in Fig. 4 together with the calculated isotonic power output. Increasing temperature increased $V_{max}$ from 4.03±0.42 $L_0$ s$^{-1}$ at 15 °C to 10.92±1.03 $L_0$ s$^{-1}$ at 30 °C (mean ± S.E.M.) (Table 3). The $Q_{10}$ for $V_{max}$ decreased considerably with increasing temperature (Table 2). The shape of the force–velocity curve as indicated by $R_P$ (Table 3) was not significantly influenced by temperature (ANOVA, $P$>0.05). Therefore, thermal effects on muscle-mass-specific maximum isotonic power output ($\dot{W}_{iso}$) are dominated by effects on $V_{max}$ with smaller contributions at 15 and 30 °C from $P_0$ (Tables 1, 2; Fig. 3).

The $Q_{10}$ for maximum isotonic power ($\dot{W}_{iso}$) decreased with increasing temperature, as did the $Q_{10}$ for $\dot{W}_{j,m}$ (Table 2). The overall $Q_{10}$ of mean $\dot{W}_{iso}$ between 15 and 30 °C was 2.27 compared with 1.74 for $\dot{W}_{j,m}$, indicating a somewhat greater overall effect of temperature on *in vitro* power output than on that found *in vivo* (Table 2). A large part of this difference was due to the greater thermal dependence of $\dot{W}_{iso}$ between 15 and 20 °C. The absolute value of $\dot{W}_{iso}$ is considerably smaller than the power output predicted from jumping distance over the entire temperature range studied (Fig. 3). The upper limit of *in vivo* power is approximately five times $\dot{W}_{iso}$ at 15 °C and three times this value at 30 °C.

The performance in one particularly long jump of 1.44 m provides striking documentation of the magnitude of the difference between *in vivo* and *in vitro* power output (Table 4). The average power during takeoff calculated for this jump (822 W kg$^{-1}$) was more than three times the maximum isotonic power estimated for the same individual at 28 °C. Peak instantaneous power during takeoff, which is

Table 3. In vitro *isotonic contractile data for the sartorius muscle of* Osteopilus septentrionalis

| $T_m$ (°C) | $N$ | $A$ | $B$ ($L_0$ s$^{-1}$) | $C$ ($L_0$ s$^{-1}$) | $R_P$ | $V_{max}$ ($L_0$ s$^{-1}$) | $\dot{W}_{iso}$ (W kg$^{-1}$) |
|---|---|---|---|---|---|---|---|
| 15 | 4 | 0.240±0.033 | 0.913±0.139 | 0.219±0.114 | 0.107±0.002 | 4.03±0.416 | 78.1±9.6 |
| 20 | 5 | 0.169±0.025 | 0.866±0.105 | 1.537±0.153 | 0.098±0.006 | 6.77±0.411 | 178.0±3.7 |
| 25 | 4 | 0.132±0.008 | 0.852±0.101 | 2.303±0.103 | 0.108±0.004 | 8.77±0.621 | 230.0±9.2 |
| 30 | 4 | 0.162±0.025 | 1.416±0.356 | 2.579±0.350 | 0.112±0.005 | 10.92±1.03 | 265.2±17.9 |

Values are given as means ± S.E.M. at each muscle temperature.

$A$, $B$ and $C$ are the constants from the hyperbolic–linear equation used to fit force–velocity data (see equation 1).

$T_m$, muscle temperature; $N$, sample size; $R_P$, power ratio (see Materials and methods); $V_{max}$, maximum velocity of shortening predicted at zero force. $\dot{W}_{iso}$, peak isotonic power output.

Table 4. *Jumping performance for one jump of 1.44 m at a* $T_b$ *of 28 °C*

| | |
|---|---|
| Measured values | |
| $M_b$ (kg) | 0.0141 |
| $L_{cm}$ (m) | 0.108 |
| $M_{hlm}$ | 0.143 |
| $L_j$ (m) | 1.44 |
| **Maximum isotonic power (W kg$^{-1}$)** | **240** |
| Predicted values | |
| $W_{j,b}$ (J kg$^{-1}$) | 7.09 |
| $W_{j,m}$ (J kg$^{-1}$) | 49.6 |
| $t_c$ (s) | 0.060 |
| **Takeoff power (W kg$^{-1}$)** | **822** |
| **Peak takeoff power (W kg$^{-1}$)** | **1644** |

Maximum isotonic power at 28 °C was estimated from measured values for the sartorius muscle of this individual at 25 and 30 °C of 223 and 254 W kg$^{-1}$, respectively, and assumed a uniform $Q_{10}$ over this temperature interval. At 30 °C, the muscle from this frog had $P_0$, $V_{max}$ and $R_P$ values of 21.9 N cm$^{-2}$, 10.92 $L_0$ s$^{-1}$ and 0.106, respectively. These values were close to the mean values for all frogs ($N$=4) at this temperature.

$M_b$, body mass; $L_{cm}$, length from the center of mass of the frog to the tip of the toes along the outstretched hindlimb; $M_{hlm}$, hindlimb muscle mass as a fraction of total body mass; $L_j$, total jumping distance; $W_{j,b}$, body-mass-specific work; $W_{j,m}$, muscle-mass-specific work; $t_c$, contact time; $P_0$, maximum isometric force; $V_{max}$, maximum isotonic shortening velocity; $R_P$, power ratio.

Power is expressed per kg of muscle mass.

predicted to be approximately twice the average power (Marsh, 1994), is thus estimated to be 1644 W kg$^{-1}$ of total hindlimb muscle mass for this jump.

## Discussion

The power required for jumping in Cuban tree frogs greatly exceeded that apparently available from the hindlimb muscles. The most powerful jumps required an average power during the entire takeoff of more than 800 W kg$^{-1}$ of muscle, and thus the predicted peak power during takeoff approached 1650 W kg$^{-1}$. This latter value exceeds by approximately sevenfold the value we measured for maximum isotonic power output in the sartorius muscle of the same animals (Fig. 3; Table 4). We consider this discrepancy in power during takeoff to be a conservative estimate for two reasons. First, our *in vivo* power is expressed relative to the total hindlimb muscle mass, and not all muscles are used to power the jump. If only 85 % of $M_{hlm}$ is involved in powering jumping, as our measurements suggest, then the peak instantaneous power would be nearly 2000 W kg$^{-1}$ of muscle for the most powerful jumps. Second, the instantaneous maximum isotonic power is likely to represent a maximal estimate of power production by the muscle. A number of factors, including the time required for activation and length–tension effects, will reduce the actual power output in a muscle undergoing significant shortening. The strength of the present study lies in the fact that jumping performance, morphological properties and contractile data were obtained on the same group of frogs. Although we did not measure contractile properties on each of the frogs used in the jumping trials, the nine animals used included many of the animals that produced the longest jumps (e.g. Table 4). We, of course, have contractile data on only one hindlimb muscle. However, we consider it extremely unlikely that the other hindlimb muscles of these frogs have contractile properties that would allow them to produce enough power directly to power the jump during the takeoff period.

The sartorius muscle is probably not involved in powering the jump (Calow and Alexander, 1973; Duellman and Trueb, 1986), but probably has properties representative of the bulk of the hindlimb muscles. The sartorius muscle was chosen for contractile measurements in this study because one can easily obtain reliable isotonic data on this muscle. Three parameters determine maximum isotonic power output, $V_{max}$, $P_0$ and $R_P$, which describes the shape of the force–velocity curve. In other anuran amphibians, the sartorius muscle has a similar fiber-type distribution to the other major hindlimb muscles (Putnam and Bennett, 1983) and, perhaps predictably, also has similar contractile properties (Marsh, 1994). For example, in *Rana pipiens*, Lutz and Rome (1994) measured a $V_{max}$ of 10.35 $L_0$ s$^{-1}$ at 25 °C in the semimembranosus muscle, a muscle definitely involved in jumping (Olson and Marsh, 1992). In comparison, Renaud and Stevens (1984) measured a $V_{max}$ of 9.76 $L_0$ s$^{-1}$ at this temperature in the sartorius muscle of the same species. Our values of $V_{max}$ for *Osteopilus septentrionalis* match those found in other comparably sized frogs (Marsh, 1994). We consider it very unlikely that our estimate of nearly 9 $L_0$ s$^{-1}$ at 25 °C is a significant underestimate of the $V_{max}$ of the other hindlimb muscles of this animal, especially considering that $V_{max}$ would have to be sevenfold higher to account for the measured peak power output during jumping. We measured a mean $P_0$ of 24.4 N cm$^{-2}$ at 20 °C and of 24.1 N cm$^{-2}$ at 25 °C, and this level of force is well within the range of values in the literature (Marsh, 1994). The highest $P_0$ values we measured on several individual preparations were approximately 30 N cm$^{-2}$, values close to the highest previously published estimates (Marsh, 1994). If 30 N cm$^{-2}$ is taken to represent the *in vivo* capacities of the muscle, our estimate of isotonic power at 25 °C would increase from approximately 230 W kg$^{-1}$ to 280 W kg$^{-1}$, a value still well below that required to produce the measured jumping distances. The highest power output measured to date in anuran muscles at 25 °C is 371 W kg$^{-1}$ for the semimembranosus muscle of the leopard frog *Rana pipiens* (Lutz and Rome, 1994). This value is only 22 % of that needed to produce the peak power required in the longest jumps by *Osteopilus septentrionalis*. Finally, our values of $R_P$ for the sartorius of *Osteopilus septentrionalis* are typical of those for other amphibian fast limb muscles.

In contrast to the present data and those of Marsh and John-Alder (1994), Lutz and Rome (1994, 1996*a*,*b*) concluded that the peak power output during takeoff of the leopard frog *Rana pipiens* could be explained on the basis of direct power output

of the hindlimb extensor muscles. They obtained an estimate of peak muscle power output during takeoff of 394 W kg$^{-1}$, which compared favorably with their estimate of 371 W kg$^{-1}$ obtained during optimal isovelocity contractions *in vitro* at 25 °C. However, the conclusions of Lutz and Rome (1994, 1996*a*,*b*) were based on jumps with a mean distance of 0.67 m. The maximum jumping distance they reported was 0.80 m, and we calculate using the methods outlined here that this would have required a peak power output of 530 W kg$^{-1}$ of muscle. This estimate is virtually identical to the value calculated from the kinematic data in Fig. 2 of Lutz and Rome (1996*a*). Other investigators have found that leopard frogs can routinely jump 1.0–1.3 m (Rand, 1952; Zug, 1978; M. M. Peplowski and R. L. Marsh, unpublished data). A jump of 1.0 m by a 25 g frog is predicted to require a peak instantaneous power output during takeoff of approximately 750 W kg$^{-1}$ of muscle, and a 1.3 m jump would require more than 1100 W kg$^{-1}$. Clearly, *Rana pipiens* are capable of producing power outputs during takeoff that are well above those expected on the basis of optimal isovelocity or isotonic contractions.

The problems encountered in analyzing the data of Lutz and Rome (1994, 1996*a*,*b*) introduce an important general issue in presenting integrative studies of muscle function during natural movements. Typically, *in vivo* performance data contain a large amount of variability (e.g. Marsh and Bennett, 1986*b*; this study). Much of this variation is probably due to muscle recruitment, i.e. the degree of behavioral motivation. Investigators must be aware of this source of variation and of the fact that individual species vary in their responses to the experimental situation, owing to behavioral or physiological factors. In some locomotor systems, recruitment may be less of an issue because the entire muscle mass is recruited as a unit, e.g. scallop swimming (Marsh *et al.* 1992) and the escape response of decapod crustaceans (Daniel and Meyerhöfer, 1989). In contrast to the behavioral data, data on muscle contractile properties are usually much less variable. This lower variability reflects to a major extent the full recruitment ensured by *in vitro* stimulation. This difference in variance was found even in the present study despite the selection of jumps that were the longest out of a series of almost 20 (Fig. 3). This being the case, the relevant comparison should be the mean *in vitro* performance with the maximal *in vivo* performance (the upper limit in Fig. 3).

If their muscles cannot produce the power required during the time available for takeoff, then how do small frogs power their jumps? Marsh and John-Alder (1994) suggested that they may use elastic elements to redistribute the work done by the hindlimb muscles. Elastic energy can be used in two ways that are not mutually exclusive. First, even if all of the work needed can be done during takeoff, energy has to be redistributed to account for the fact that the mechanical power rises to a peak late in takeoff (Marsh and John-Alder, 1994). This potential function of series elasticity has been realized for many years (Hill, 1950). Second, energy may be stored prior to any movement of the center of mass, i.e. before takeoff actually begins, a mechanism previously demonstrated in insects

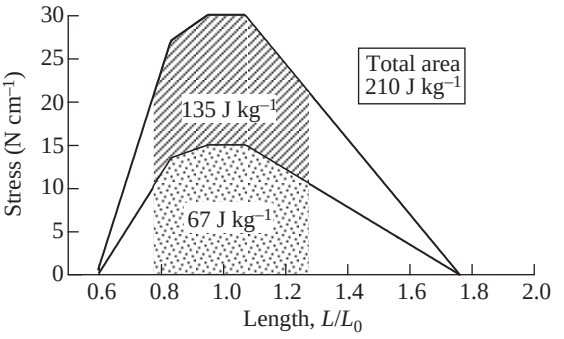


Fig. 5. Representative length–tension curve for vertebrate muscle. This curve (upper line) is based on the standard single-fiber length–tension curve for frog skeletal muscle (see Woledge *et al.* 1985) and assumes a maximum isometric force $P_0$ of 30 N cm$^{-2}$. The maximum work theoretically attainable for such a muscle contracting infinitely slowly throughout the range of lengths shown is 210 J kg$^{-1}$. The hatched area represents a more realistic degree of shortening (50 % strain) and yields a maximum work output of 135 W kg$^{-1}$. However, during rapid shortening, force is probably reduced by 50 % or more due to force–velocity effects, resulting in a predicted maximum work output of 67 W kg$^{-1}$ (dotted area).

(Bennet-Clark and Lucey, 1967; Bennet-Clark, 1975) and referred to as the catapult mechanism.

Of course, using elastic storage does not change the work output required from the muscles, it simply redistributes this work in time. Therefore, we can ask whether the work output of the muscles is a reasonable value. Considering that the work was performed by the total hindlimb musculature, the highest work outputs we measured were approximately 50 J kg$^{-1}$ of muscle. If, as suggested above, only 85 % of the total hindlimb muscle mass is used during jumping, this estimate is increased to approximately 60 J kg$^{-1}$. This value is high, but within the limits of what may be expected from frog skeletal muscle. This conclusion can be reached by the following analysis. As has been pointed out many times, the maximum theoretical work output of a muscle can be calculated by integrating the area under the length–tension curve. If one assumes the standard length–tension curve (Woledge *et al.* 1985) for frog muscle (Fig. 5) and a perhaps somewhat optimistic $P_0$ of 30 N cm$^{-2}$, then the total area under the curve is equivalent to approximately 210 J kg$^{-1}$ of muscle (after conversion to appropriate units). This amount of work is actually impossible to obtain under realistic conditions because the muscle would have to shorten infinitely slowly from a length of 100 % above $L_0$ to a length of 40 % below $L_0$. Muscles *in vivo* cannot shorten either that slowly or over that large a strain. If one takes as a maximum possible strain a value from 25 % above $L_0$ to 25 % below this length, then the area under this section is equivalent to approximately 135 J kg$^{-1}$. For muscles such as those used in frog jumping that must produce significant power outputs, this maximum is further reduced because of force–velocity effects. Assuming that the muscle can maintain 50 % of its maximum force over the whole range of shortening, then an estimate of 67 J kg$^{-1}$ is

obtained. Even this estimate may be optimistic as strains as large as 50 % have never been measured during natural movements, and 30 N cm$^{-2}$ is a rather high estimate for $P_0$. Thus, our measurement of 50–60 J kg$^{-1}$ is impressive, but certainly within the theoretical capacities of frog muscle.

Interestingly, the work output of the hindlimb muscles is temperature-dependent (Fig. 2). This conclusion follows from the temperature effects on jumping distance (Fig. 1), because jumping distance is linearly related to the work done. The thermal effect on muscle work output is intriguing, because it is not predicted from the effects of temperature on $V_{max}$. If a muscle shortens at the same relative point on the force–velocity curve (measured as $V/V_{max}$), and shortens by the same distance, then the work done should be approximately the same. Work output should be similar because temperature does not have a major influence on $P_0$ or on the shape of the force–velocity curve. Therefore, at the same $V/V_{max}$, the force will be approximately equal at different temperatures and, because work equals force times distance, the work done will be equivalent. Of course, at lower temperatures, this work would be done more slowly (lower power output) because of the lower absolute velocity of shortening. Clearly, this straightforward reasoning from muscle properties does not apply to frog jumping. Instead, in Cuban tree frogs, as in other frogs (Marsh, 1994), increasing muscle temperature improves the shortening conditions for the hindlimb muscles in terms of producing work.

Reduced work output at lower temperatures could result from reduced amounts of shortening or lower average force during shortening. Frogs appear to extend their legs fully during jumping over a wide range of temperatures, which should result in the same amount of shortening of the muscles. This observation is confirmed by the data of Lutz and Rome (1996*a*) on the semimembranosus muscle. Very probably then, the reduced work output at lower temperatures is due to lower force production. The data of Lutz and Rome (1996*a*,*b*) provide one possible explanation for this lower force production. They estimate that the semimembranosus muscle of *Rana pipiens* shortens at $0.45V/V_{max}$ at 15 °C and at $0.32V/V_{max}$ at 25 °C. As pointed out by Lutz and Rome (1996*b*), power output is nearly optimal at both of these relative velocities. However, the higher $V/V_{max}$ at the lower temperature would reduce force during shortening to only approximately 50 % of the value at 25 °C, thus greatly reducing the work output for the same shortening distance. We do not expect that all of the muscles in the hindlimbs of jumping frogs shorten exactly like the semimembranosus of *Rana pipiens*. Nevertheless, we do conclude that the biomechanics of the system must be tuned to the kinetics of the hindlimb muscles in such a way as to limit $V/V_{max}$ and thus to maintain high force production during shortening. This tuning is apparently disturbed by decreasing temperature, which slows the absolute muscle kinetics, but leaves unchanged other important parameters, such as body mass, muscle moment arms and the elastic properties of muscle tendon units.

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